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Variation in Growth Rate and Reproduction of the Bryozoan *Bugula neritina*

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Abstract. Colonies of the arborescent cheilostome bryozoan *Bugula neritina* vary dramatically in their growth rate even when in apparently identical microhabitats. Comparison of growth rates of juveniles derived from four parent colonies at each of two sites showed only weak effects of parental colony on juvenile growth. These effects accounted for at most only 5.4% of total variation in growth. Variation in growth, and hence age at first reproduction, is interpreted as a plastic response of colonies to fine-scale environmental variation.

Bryozoans from seagrass meadows mature at a smaller size than those colonies from nearby rocky reefs (1200, *vs.* 3500 zooids at first reproduction, respectively). When juveniles from both of these habitats were grown in a common garden, there was, again, no variation among parental groups, but a highly significant effect of origin of juveniles. Juveniles matured at a size similar to that seen in their parental population, indicating that genetic or very early maternal effects influence timing of reproduction.

A *post hoc* test of the effect of onset of reproduction on colony growth showed no reduction in growth rate. Instead, colonies that reproduced grew faster than similar aged and sized colonies that did not reproduce.

Introduction

A growing body of empirical evidence suggests that, for modular organisms, many demographic variables depend more strongly on size than on age. Three of the most important such variables are mortality rates, timing of onset of reproduction, and reproductive output. Mortality rates are often size-dependent in two ways; first, the probability of a colony being eaten or overgrown may decrease with increasing size (*e.g.*, Reiswig, 1974; Werner and Caswell, 1977; Gross, 1981; Antonovics and Primack, 1982; Russ, 1982; Sebens, 1982; Hughes and Jackson, 1985; Hughes and Connell, 1987). Second, small colonies may be killed completely when attacked, while a similar attack on a larger colony may only cause damage ("partial mortality"), from which the colony subsequently recovers (Bak *et al.*, 1981; Palumbi and Jackson, 1982). Size, rather than age, may determine the onset of reproduction for many clonal animals and plants (Inouye and Taylor, 1980; van Duyl *et al.*, 1981; Gross, 1981; Wahle, 1983; Augspurger, 1985; Keough, 1986; but see Harvell and Grosberg, 1988). For a number of clonal organisms, size is correlated positively with reproductive output (Hayward, 1973; Inouye and Taylor, 1980; van Duyl *et al.*, 1981; Nakauchi, 1982; Sebens, 1983; Wahle, 1983; Augspurger, 1985), which in turn is thought to be an important component of relative fitness.

A negative correlation between size and mortality and a positive correlation between size and reproductive output both favor rapid initial growth of juveniles. However, many clonal organisms show extensive variation in growth rate. Harper (1977; 1985) reviews data for terrestrial plants, and Hughes and Jackson (1985), Jackson and Winston (1982), and Keough (1986) provide examples of such variation in clonal marine animals. For most marine organisms, the causes of this variation have not been examined in enough detail to estimate relative contributions of phenotypic responses to fine-scale environmental variation and genetic or maternal factors. For many plants, however, considerable variation in morphology and growth can be attributed to phenotypic plasticity in response to small-scale environmental variation (Silander, 1985). In animals, both genetic and environmental influences on growth rate are reported commonly (*e.g.*, Travis *et al.*, 1987).

The cosmopolitan bryozoan *Bugula neritina* appears

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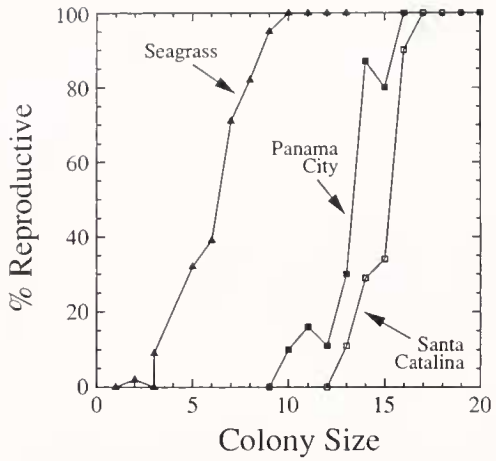

Figure 1. Onset of reproduction in *Bugula neritina*. The figure shows the percentage of colonies reproductive as a function of size for: Solid triangles: colonies in seagrass in the northeastern Gulf of Mexico. The curve is a composite from the sites and experiments reported elsewhere (Keough, 1986, Keough and Chernoff, 1987). n > 1000. Solid squares: colonies living on rock surfaces at Panama City, Florida. February 1986, n = 154. Open squares: colonies living on rock surfaces at Santa Catalina Island, California. Data from Keough (in prep.). n > 500.

to fit these emergent generalizations for clonal organisms. It is an arborescent species, in which a single colony represents the genet. Neither regrowth from dispersed fragments nor fusion between neighboring colonies has ever been observed. Fertilization is internal and larvae are brooded singly by maternal zooids in hyperstomial ovicells. The relatedness between larvae within a single colony is unclear; barring somatic mutation, the maternal zooids are genetically identical, but the number of paternal genotypes is unknown. Larvae from a single colony are at least half-sibs and at most full sibs. The onset of reproductive activity is more closely associated with size than with age, and survivorship increases with some function of size or age (Keough, 1986; Keough and Chernoff, 1987). In this paper, I re-analyze earlier data to show effects of both size and age on survivorship. When colonies are small, they suffer complete mortality, while larger colonies are frequently damaged, rather than killed outright (Keough, unpub. ob.). Growth rates vary extensively within cohorts, even when colonies are growing in what appears to be a relatively homogeneous habitat—the distal tips of artificial seagrass leaves (Keough, 1986). Similar variation occurs among cohort members attached to rock surfaces (Keough, 1989).

In addition to variation within populations, size at first reproduction also varies among populations. *Bugula neritina* colonies from seagrass meadows in the northeastern Gulf of Mexico grow rapidly in spring and fall, reproduce while small, and generally are short-lived, probably because their substratum is ephemeral (Keough, 1986; Keough and Chernoff, 1987). In contrast, colonies living on rock faces in southern California grow large, do not reproduce until they are large, and live considerably longer than one year (Keough, 1989). At Panama City, in the northeastern Gulf of Mexico, colonies live on large permanent structures, including artificial reefs, natural limestone outcroppings, and rock jetties. In this habitat, the demography of *B. neritina* appears closer to that seen in southern California (Fig. 1): they grow large, and appear not to reproduce while small.

What are the causes of this demographic variation? Here I describe experiments to determine causes of variation in growth rate and size of reproduction. I partition within-cohort variation in post-settlement growth rate of juveniles into variation occurring among and within maternal colonies, with the aim of detecting genetic components of growth rate. I also examine the basis of geographic variation in size at first reproduction.

Materials and Methods

To distinguish between effects of age and size on survivorship, I re-analyzed data from *Bugula neritina* colonies in seagrass meadows in Florida. In these experiments, cohorts of juveniles were established in the laboratory, then transplanted to the field and monitored (see Keough, 1986 for details). At any point in time, then, the experimental population comprised colonies from earlier cohorts that had grown rapidly (large, old), similar, slower-growing colonies (small, old), and small, young colonies from later cohorts. For colonies living in seagrass meadows, survivorship appears dependent on both size and age (Fig. 2).

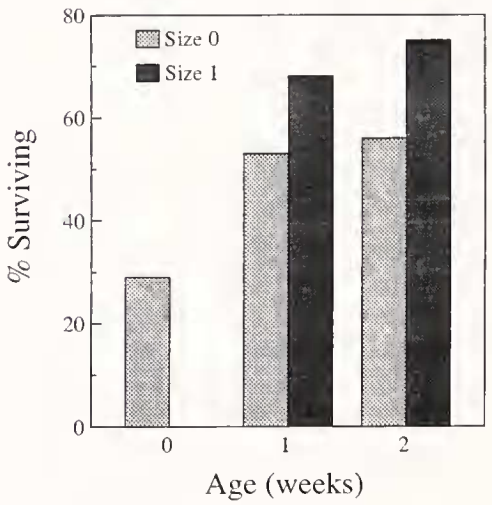

Figure 2. Effects of age and size on survivorship of *Bugula neritina* colonies. Histograms show probabilities of survival for juveniles of different sizes from a single experimental cohort, and juveniles of the same size, but of different ages. Data were taken from Keough (1986).

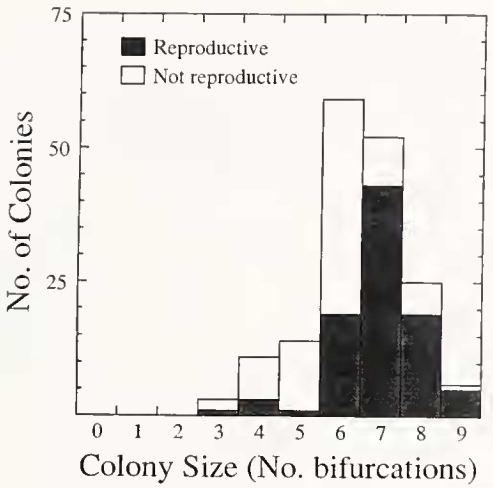

Figure 3. Reproduction as a function of size in *Bugula neritina* colonies under experimental conditions. Data are shown for experimental juveniles from Panama City after 5 weeks, and for natural recruits derived from Alligator Point after the same period of time.

Variation in growth

At the time of the first experiment (25 March 1986), there were no mature *Bugula neritina* colonies in seagrass meadows or at Alligator Point marina, which had been the source population for other demographic work (Keough, 1986; Keough and Chernoff, 1987), and where colonies mature at the same size as those from seagrass meadows (Keough, unpub. obs.). Therefore, I collected colonies from a sunken barge approximately 4 km off Panama City, at a depth of 20 m. Parental colonies were separated from each other by >10 m, to reduce the chance that they were closely related. After 2 days in the dark, the colonies were exposed to bright light and the four colonies that released the most larvae were used in the experiment.

Four or five larvae from a given colony were pipetted individually into a sterile plastic petri dish (50-mm diameter) containing seawater, and allowed to settle and metamorphose. Juveniles close to the edges of plates were removed. Without removing it from the water, each dish then had a 4-mm hole drilled into its center, and was bolted to a 60 × 20 cm piece of clear plexiglass. Each plexiglass sheet held 16 dishes in two rows of 8, with 4 dishes from each parental colony. The dishes were not arranged randomly, but in four 2 × 2 arrays, each array containing one dish from each parental colony. Two of the arrays were at ends of the plexiglass plates, and the positions of the dishes were further constrained so each parent appeared once at the corner of a plate and three times away from the corners. This design ensured that any micro-environmental variation could not bias the outcome of the experiment.

The plexiglass plates were then transported in seawater to a study site in the *Thalassia* meadow at Lanark, 1 km from the F.S.U. marine laboratory (see Keough and Chernoff, 1987, for a description of this site). There, they were bolted to a 1-m^2 PVC frame, the legs of which had been driven into the sediment until the frame was approximately 15 cm above, and parallel to, the substratum. All fasteners used in the experiment were stainless steel. The petri dishes faced downwards, with the plexiglass above them, because Young and Chia (1984) have shown that sedimentation can be a major source of mortality for some newly settled sessile animals, and my aim was to maximize the number of juveniles available for growth measurements.

At weekly intervals I returned, unbolted the plates, and transported them back to the laboratory, where I measured each juvenile. The plates were kept in running seawater, from which they were never removed for more than a few seconds.

Bugula neritina colonies in north Florida grow with regular bifurcations. New pairs of zooids are produced (budded) at the distal tip of each branch, with usually four pairs of zooids (budding events) between each bifurcation point (see Keough and Chernoff, 1987, their Fig. 2, for more details). Unless the colony has been damaged, each branch is approximately the same size, and the colony can be viewed as a series of distal buddings, with "waves" of bifurcations at regular intervals. I measured size by counting first the number of bifurcation waves and then the number of zooid pairs at the growing tip of each branch, *i.e.*, the number of budding events since the last bifurcation. This measurement can be used to estimate either the number of zooids or to compute the number of times the colony has budded. Thus, a colony of size 3.2 (bifurcated 3 times, with 2 further zooid pairs after the last bifurcation point) has budded 14 (*i.e.*, 3 bifurcations × 4 zooids/bifurcation + 2 zooids) times, and has 88 zooids. When measuring each colony I noted any missing branches, pale colored zooids, partial fouling, and the presence or absence of embryos.

After the third week, some of the juveniles were approaching a size at which they grew close to their neighbors, so I reduced their numbers to 1 or 2 per dish.

In the first experiment I used 5 such plates, with a total of 247 juveniles, distributed approximately equally among the 4 parents (57, 73, 57 and 60 juveniles).

Three weeks into the experiment, I obtained fertile colonies from Alligator Point and did a second experiment, using four parental colonies and four plexiglass sheets. The protocol for this experiment was identical to that of the first one, with colonies retained in collecting buckets for a period similar to travel time from Panama City to the laboratory, and the experiment began on 15 April

1986. There were 43, 51, 39, and 51 juveniles from the four parents.

Analysis

The plexiglass plates were a logistical convenience and were almost touching each other. They were not replaced in the same arrangement each week. A preliminary analysis of variance for the first week's growth, using mean growth of all juveniles in a dish as the dependent variable, showed neither a significant effect of plates nor a parent × plate interaction. For these reasons, I ignored plates in the analysis, and had simply a nested design, with juveniles within petri dishes within parents. The juveniles were small and well-separated from each other, so I did not expect juveniles to interfere with each other so as to make their growth non-independent. Any correlation among juveniles within a dish should reflect common responses to microhabitat conditions within dishes. This assumption does not affect the test of the main hypothesis about parental colonies, however, because growth rates of individual juveniles within dishes are not used to test the effect of parents (which is tested using variation among dishes).

I used the number of budding events as the measure of growth. Two analyses are possible from this experimental design. First, the weekly growth increment of each juvenile can be used as the dependent variable in a series of separate analyses for each week. This experiment is a simple nested design (juveniles within dishes, dishes within parent colonies), and has the drawback that statistical tests based on each week may not be independent, if juvenile growth over one period influences subsequent growth. This analysis cannot detect juveniles that grow consistently faster or slower, in successive weeks. The alternative analysis is to use only those juveniles that survived undamaged and were not culled, in a repeated measures analysis, with weekly growth increment as the dependent variable. The design is complicated, with nested factors (dishes) and repeated factors (weeks), and has two deficiencies; first, no information is gained from colonies that may have survived for most of the time, but were culled or damaged late in the experiment. The power of the analysis of very early growth is reduced by the decreased sample sizes. Second, repeated-measures analyses of variance have restrictive assumptions about the structure of covariance matrices (Winer, 1971), and the levels of the repeated factor (weeks) are always applied in a fixed, rather than random, order.

Here, I present the results of both sets of analyses, but their relative strengths and weaknesses must be considered.

Table I

Analysis of weekly growth increments for Bugula neritina *colonies from Panama City*

Variable	Week after settlement 1	2	3	4	5
Mean squares					
Among parent colonies	9.7	0.5	26.3	104.4	30.7
Dishes within colonies	2.9	7.4	26.5	78.2	57.5
"Siblings" within dishes	1.4	7.5	25.0	42.8	51.6
Degrees of freedom					
Parent colonies	3	3	3	3	3
Dishes—actual (quasi)	71 (64)	71 (58)	68 (57)	67 (57)	61
Juveniles	172	163	154	113	67
F-statistics					
Colonies	3.2*	0.1 ns	1.0 ns	1.2 ns	0.5 ns
Dishes 2.0***	1.0 ns	1.1 ns	1.8*	1.1 ns	
Variance components					
Colonies	5.4	0.0	0.0	0.8	0.0
Dishes within colonies	22.4	0.0	1.8	24.2	5.5
Siblings within dishes	72.2	102.3	98.2	75.0	96.1

The dependent variable was the number of budding events in the week concerned. The analysis was a 2-level nested analysis of variance with unequal samples sizes, using quasi F-ratios to test the main effect of parental colonies. The table shows F-ratios, mean squares, degrees of freedom, and estimated variance components. The degrees of freedom are also shown for the composite denominators used to test the main effect of parental colonies. ns, $P > 0.05$; *$0.05 > P > 0.01$; **$0.01 > P > 0.001$; ***$P < 0.001$.

Size at first reproduction

At the beginning of the experiment there was natural recruitment onto the petri dishes and the plexiglass plates. These larvae were probably produced by the population established at the Lanark site during a previous experiment using Alligator Point parents (Keough and Chernoff, 1987). To make a comparison of the size at first reproduction between colonies from Panama City and those occurring within seagrass meadows, I recorded the positions of some of these early recruits. Up through the fourth week I recorded the sizes of any *Bugula* colonies that were reproductive. In the fifth week I identified each natural recruit that had bifurcated more than four times and measured its exact size and reproductive condition.

Results

The growth rates of progeny from different Panama City colonies varied little. Only in the first week after settlement was there significant heterogeneity among parental colonies (Table I), and even then, only 5.4% of the total variation in growth rates was accounted for by parent colonies. The repeated measures analysis of vari-

Table II

Repeated measures analysis of variance using weekly growth increments of all Bugula *colonies that survived undamaged to the end of the experiment*

Source of variation	Panama City			Alligator Point		
	DF	MS	F	DF	MS	F
Among colonies	3	3.20	1.34 ns	3	11.85	4.92**
Siblings within colonies	80	2.39		145	2.41	
Among weeks	4	107.94	20.11***	1	159.25	51.84***
Colonies × weeks	12	4.36	0.81 ns	3	9.62	3.13***
Weeks × siblings	320	5.37		145	3.07	

Data were unbalanced, and sums of squares were computed by unweighted means (Winer 1971). ns, $P > 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

ance using only those juveniles that survived undamaged for 5 weeks showed no significant heterogeneity among parents, but highly significant variation with time (Table II). Inspection of mean weekly growth increments showed that the means did not differ by more than 1.5 buddings for the first few weeks (Table III). The clearest trend was a decline in the mean growth through the experiment, accompanied by a substantial increase in the variance (Table III).

For the juveniles from Alligator Point, the repeated measures analysis showed a highly significant effect of parent colony on growth rates (Table II), but individual weekly analyses showed only a single significant result, with parental colonies explaining a maximum of 7.4% of growth variation (Table IV). Inspection of means showed that the differences among colonies were slight in the first week after settlement and larger in the second week, although variances increased during the second week (Table III).

In both experiments, variation among dishes of juveniles from the same parent colony accounted for 15–20% of growth variation (Tables I, II, IV).

Mortality of the juveniles in this protected environment was usually <5% per week (Table V). Almost 80% of the Panama City juveniles survived for the 5 weeks of the experiment. There was no significant variation in post-settlement mortality among parental groups for the Panama City experiment, but slight variation among Alligator Point colonies (Table V). This latter result was caused by a single colony, the progeny of which suffered 23% mortality. The other three colonies did not differ significantly in the mortality rate of their juveniles ($G = 3.62$, $df = 2$, $P > 0.10$).

Panama City colonies had embryos by the fourth week, and many (46% of 154 colonies) were reproductive after the fifth week. The proportion of reproductive colonies increased with colony size (Fig. 2), and the mean size at first reproduction was 7.3 bifurcations (31.3 buddings, SD = 3.27, n = 92). Natural recruits matured at a smaller size, with a mean of 6.1 bifurcations (*i.e.*, 25 buddings, SD = 3.18, n = 58). Although most colonies were fouled by late May, there were a few unfouled Alligator Point colonies that began to reproduce. These colonies matured at a size similar to the naturally recruited juveniles (mean size at 1st reproduction 5.2, 22.3 buddings, SD = 2.6, n = 7). The natural recruits and Alligator Point juveniles did not differ significantly from each other, but both differed from the Panama City juveniles (single factor analysis of variance with unequal sample sizes, using size at first reproduction as the dependent variable, $F_{2,154} = 82.7$, $P \ll 0.001$; SNK procedure indicated that natural and Alligator Point means differed from Panama City at $P = 0.001$).

Colonies became fouled by algae during the later stages of both experiments, and large colonies often lost branches. Eight of the 21 Panama City juveniles that had begun to reproduce by the end of the fourth week had all reproductive structures removed during the fifth week, leaving them as small, asymmetric colonies.

There was no major reduction in colony growth rate associated with the onset of reproduction. No colony reproduced within the first three weeks, so I compared the growth rates of colonies that eventually reproduced to the rates of colonies that failed to reproduce. I used the growth rate for the first three weeks as a measure of pre-reproductive growth rate, and weeks 4–5 to estimate "post-reproductive" growth rates. I pooled data across parent colonies, since that factor accounted for little variation in growth rate. For each colony I used the mean growth rate for the first three weeks and the mean growth rate for weeks 4–5, and I analyzed the data using a repeated measures analysis of variance with two factors: presence or absence of reproduction, and growth period (pre- and post-reproduction). Only undamaged colonies were used in the analysis. Surprisingly, colonies that reproduced showed slightly increased growth at the onset of reproduction, while those that did not reproduce had a diminished growth rate in weeks 4 and 5 (Table VI).

Size at first reproduction was not significantly heterogeneous among parental groups for the Panama City juveniles (single factor analysis of variance using undamaged colonies, $F_{4,87} = 2.216$, $P = 0.074$). The number of reproductive colonies from the Alligator Point experiment was too small for such an analysis. Size at first reproduction was independent of growth rate for the Panama City juveniles: using mean growth rate for the first two weeks and size at first reproduction, $R^2 = 0.007$. The only significant correlation was between growth rate and age at first reproduction ($R^2 = 0.07$, $r = -0.239$, $n = 92$, $P = 0.02$), and even that relationship was weak. These

Table III

Mean weekly growth increments for Bugula *colonies from Panama City and Alligator Point*

Colony		Weeks 1	2	3	4	5
Panama City						
1	X	8.3 (1.5)	5.7 (3.1)	3.6 (3.9)	4.0 (7.5)	3.8 (7.1)
	n	57	53	48	39	26
3	X	8.3 (1.4)	5.7 (2.2)	3.0 (5.0)	2.3 (8.9)	2.7 (7.5)
	n	73	72	71	59	41
4	X	7.5 (1.1)	5.9 (2.1)	2.2 (6.5)	3.2 (7.5)	1.9 (7.9)
	n	57	57	55	43	30
6	X	7.7 (1.4)	5.7 (3.4)	3.7 (4.2)	5.8 (4.8)	4.0 (6.9)
	n	60	56	52	43	35
Alligator Point						
3	X	7.0 (1.7)	8.2 (3.5)			
	n	30	40			
4	X	6.2 (1.1)	6.4 (5.0)			
	n	51	48			
5	X	6.4 (1.6)	4.4 (7.1)			
	n	39	35			
6	X	6.5 (1.3)	5.7 (4.5)			
	n	51	47			

Data were means of the number of budding events, with standard deviations in parentheses. All undamaged colonies were included in each week, regardless of their subsequent fates.

relationships are as expected when size, rather than age, is important.

Discussion

The two demographic variables described in this study showed contrasting patterns of variation. Growth rates were very plastic, varying primarily among juveniles from the same parent, with only a minor component of variation that could be ascribed to parental colony, and little apparent variation between colonies from the two collection sites. In contrast, size at first reproduction varied strikingly among the progeny of colonies from two different sites, but showed relatively little variation within populations.

The experiments were designed to partition variation in juvenile growth into that occurring among and within "sibships." It is unclear whether these juveniles are closer to half or full sibs, because of uncertainty about the method of fertilization in most bryozoans; for *Bugula neritina*, electrophoretic attempts to resolve paternity have been thwarted by low levels of variability and few useable allozymes (Keough, unpub. obs.).

Variation among sibships reflects mostly maternal (genetic + maternal environmental), and possibly paternal genetic, effects, while variation within sibships should reflect phenotypic plasticity, genotype-environment interactions and paternal effects. In the "common garden" environment used in this study, there was little evidence of any maternal component, and, therefore, little evidence of additive genetic variation in growth rate. The largest amount of growth variation attributable to maternal colonies in any one week was 7.2%. Even when there were visible differences in mean growth rates of juveniles in a particular week, the rank order of sibships was not

Table IV

Analyses of weekly growth for Bugula neritina *juveniles from Alligator Point*

Source of variation	DF	MS	F	Var. Comp
Growth—Week 1				
Among colonies	3	5.6		2.9
Dishes within colonies	58 (54)	2.8	2.0 ns	17.3
"Siblings" within dishes	122	1.7	1.6*	79.9
Growth—Week 2				
Among colonies	3	95.3		5.1
Dishes within colonies	58 (51)	35.2	2.6 ns	19.8
"Siblings" within dishes	108	20.5	1.7*	72.2

The dependent variable was the number of buddings, and the analysis was a 2-level nested analysis of variance with unequal samples sizes, using quasi F-ratios to test the main effect. The table shows F-ratios, mean squares, degrees of freedom and variance component analysis. The degrees of freedom are also shown in parentheses for each composite denominator used to test the effect of colonies. ns, $P > 0.05$; *$0.05 > P > 0.01$.

Table V

Weekly mortality of juveniles from different Panama City and Alligator Point parents

Colony #	1	2	3	4	5	Total
Panama City						
1	10.0 (57)	3.5 (57)	3.6 (55)	15.2 (46)	2.3 (43)	16.0 (50)
3	0.0 (73)	1.4 (73)	6.9 (72)	12.5 (64)	4.2 (48)	19.0 (62)
4	0.0 (57)	1.8 (57)	12.5 (56)	9.5 (42)	5.4 (37)	25.8 (49)
6	0.0 (60)	5.0 (60)	8.8 (57)	4.2 (48)	2.2 (46)	28.6 (53)
Pooled	0.0 (247)	2.8 (247)	6.7 (240)	8.8 (217)	3.4 (174)	21.7 (214)
Alligator Pt						
3		2.3 (43)				
4		11.8 (51)				
5		23.1 (39)				
6		9.8 (51)				
Pooled		11.4 (184)				

All juveniles were pooled, regardless of dishes. Mortalities are shown as percentages, with sample size in parentheses.
G-test to compare mortality among colonies: Panama City, $G = 4.37$, $df = 3$, $P > 0.1$; Alligator Pt, $G = 9.0$, $df = 3$, $P < 0.05$.

maintained in subsequent weeks, so no groups of juveniles grew consistently faster than others. Usually about 20% of variation in growth was attributable to dishes, suggesting that there may have been slight differences in microhabitat among dishes. However, most of the variation occurred among related juveniles within single petri dishes. The causes of this latter variation are unclear. In the presence of apparently strong selection for rapid growth rates, it is not surprising to find little remaining variation that could be attributed to maternal genetic effects (Fisher 1958). However, responses to selection on single traits, such as growth rate, may depend on selection of other traits (Via and Lande, 1985), and small negative genetic correlations between traits may retard approaches to selective equilibria.

There was no noticeable difference in growth rate between juveniles from the two sites, although both cohorts showed variation through time. I have previously shown considerable seasonal variation in juvenile growth of cohorts from the Alligator Point population (Keough, 1986).

Juveniles suffered very low mortality over five weeks. The cumulative mortality over this whole period was less than most weekly mortality rates for juveniles transplanted onto distal sections of artificial seagrass leaves at the same site (Keough, 1986; Keough and Chernoff, 1987). All of these juveniles were handled in the same way. The petri dish experiments demonstrate at least that the mortality of juveniles on seagrass leaves is not a handling effect, but represents the action of crawling predators, sedimentation, or abrasion of leaves, because these processes were prevented from occurring on the petri dishes. Algal growth may kill juvenile ascidians (Young and Chia, 1984), but algae seem unimportant in my study, because the petri dishes had markedly higher standing crops of algae than do seagrass mimics or natural *Thalassia* leaves.

Growth rates of juveniles attached to artificial seagrass blades are more variable than those of juveniles in petri dishes (*cf.* Keough, 1986; Keough and Chernoff, 1987). On seagrasses, by the time the first juveniles begin to reproduce, others may not have grown since settlement. The greater variation in growth may be due to an environmental difference between the inverted petri dishes and the distal 10 cm of plastic seagrass mimics, or, more precisely, that the seagrass mimics, and by implication, seagrass leaves, are a more variable environment than the petri dishes. The two sets of experiments were done in different years, and food supply *may* have been more variable in 1985, when artificial seagrasses were used, than in 1986 in the petri dishes. However, similar results from another seagrass site in other seasons and in California suggest that juveniles on substrata mimicing natural ones generally show extensive within-cohort variation in growth (Keough, 1986; Keough and Chernoff, 1987; Keough unpub. obs.). Why do juveniles on the same part of a seagrass blade have such disparate growth rates? One plausible reason may be that the hydrodynamic "neighborhood" of a leaf is likely to vary both temporally and spatially, depending on local weather and growth and loss of surrounding blades. A single bryozoan probably experiences a range of conditions, so plasticity of growth may be more likely than specialization. Theoretical considerations of the evolution of plasticity focus on variation between, rather than within, environments (Via, 1987; Via and Lande, 1985), with genotypes dispersing between environments. It may be that for many sessile animals, dispersal between habitats, such as Alligator Point and Panama City, is rare, but that there is substantial small-scale variation within environ-

Table VI

Growth of Bugula *juveniles before and after the onset of reproduction*

Source of variation	DF	MS	F
Reproductive group	1	13.15	10.64**
Juveniles within reprod. gps	85	1.23	
Before/after onset of reprod.	1	0.47	0.26 ns
Reprod. group × onset	1	16.07	8.92**
Onset × juveniles	85	1.80	
	Wks 1–3	Wks 4–5	n
Reproduced	6.32	6.88	62
No reproduction	6.39	5.60	25

The analysis was a repeated measures analysis of variance, comparing the growth of juveniles that did and did not reproduce. The dependent variable was the average weekly growth (no. of buddings) of juveniles; the repeated measure was the growth of juveniles before (weeks 1–3) and after (weeks 4–5) the onset of reproduction. Only undamaged colonies were used in the analysis. Data were unbalanced, and sums of squares were computed by unweighted means (Winer, 1971). The figures beneath the analysis of variance table are treatment means. ns, $P > 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

ments. This possibility seems worthy of further investigation.

The two cohorts differed in their mean size at first reproduction, with the juveniles from the Panama City rocky reef maturing at a larger size than those from Alligator Point (31 *vs.* 25 budding events). The number of zooids increases exponentially with the number of buddings, so this apparently small difference is equivalent to Alligator Point colonies maturing after producing around 1200 zooids, while those from Panama City did not reproduce until they had >3500 zooids. The growth rates of the two cohorts were similar (Alligator Point colonies actually grew slightly faster), so Panama City colonies reproduced at least a week later than those from Alligator Point.

A difference in onset of reproduction is consistent with other life history differences between the two populations; on seagrasses, *Bugula* colonies are necessarily short-lived because of the ephemerality of their substratum. They grow rapidly, and never get very large. The largest colonies have branched 12 times, but these colonies are rare (Figs. 4, 8 in Keough and Chernoff, 1987). In contrast to seagrasses, rocky reefs and jetties are more permanent habitats. Colonies near Panama City and at Santa Catalina Island are more long-lived: newly settled colonies have survived at Santa Catalina Island for >1 year (Keough, unpub. obs.), by which time they were still considerably smaller than the largest colonies observed at that location. Colonies on rocky substrata also grow much larger than colonies on seagrasses, branching at least twice as many times, resulting in at least three orders of magnitude more zooids. Because these animals are clonal and most zooids bear embryos, later reproduction results in more embryos per colony. Thus, rocky reef *Bugula* have an early commitment to asexual (clonal) propagation of zooids, with later sexual, dispersive propagation.

Natural recruitment allowed me to test for any effect of transplantation by comparing the experimental cohorts and the natural juveniles drawn from parent colonies on seagrass. This comparison showed that transplanting had no substantial effect on size at first reproduction.

In both experimental cohorts, the juveniles matured at approximately the same size as did colonies in their parental populations, suggesting a maternal component to size at first reproduction. It is impossible to determine whether this is a genetic or environmental effect, since *Bugula* larvae develop completely within maternal ovicells. For some solitary species, egg size can have a strong influence on larval morphology and development (Sinervo and McEdward, 1988), but there are no comparable data for clonal species. It is not clear how maternal environmental effects on 400-μm larvae might influence size at first reproduction, since by this time even colonies from seagrass meadows have >1200 asexually produced zooids. I suggest that a substantial genetic component to size at first reproduction is more likely, but there are no data to resolve this question.

Reproduction did not result in any reduction in growth rate; rather, those colonies that began to reproduce actually grew faster after the onset of reproduction, while those not reproducing had a reduced growth rate during the same period. The latter observation is not surprising; failure to reproduce may be a result of insufficient food early in life or disease, which may subsequently cause reduced growth. The experiment provides no evidence for a major cost associated with reproduction. When a colony reproduces, >50% of zooids may bear spherical, 400-m diameter embryos, whose tissue masses probably exceed those of the maternal zooids. Production of larvae seems such a substantial investment of resources that it is perhaps surprising that the allocation of considerable resources for the production of embryos had no effect on the absolute amount of resources devoted to clonal growth.

Although growth variation and its causes have been examined in detail for many terrestrial and freshwater organisms (Berven and Gill, 1983; Travis, 1983), such studies are less common in marine environments. There exist relatively few documentations of the extent of growth variation that is not associated with obvious environmental gradients (*e.g.*, Koehn *et al.*, 1980; Levinton, 1983; Levinton and Monahan, 1983), or interactions with similar organisms (Peterson, 1982; Wethey, 1982), and the causes of this variation are obscure. In this case,

Bugula do not interact strongly with other sessile organisms because of the abundance of free space on seagrass leaves (Chernoff, 1985), and although some growth variation can be explained by basal-distal gradients in physical conditions (see Luckenbach, 1984; Eckman, 1987, for a discussion of flow effects), there remains a substantial amount of growth variation that presumably is a response to fine-scale environmental heterogeneity. I suggest that the variability of their environment on very small scales reduces the likelihood of within-population genetic differentiation of growth rate.

On larger, between-population scales, variation in reproductive variables is also well documented in other habitats, and is often associated with strong selection. Some marine species may switch between planktotrophy and lecithotrophy over parts of their range (Eyster, 1979) or within populations (Levin, 1984), or individuals may have the capacity to switch between iteroparity and semelparity in response to food availability (McKillup and Butler, 1979). In the present case, longevity of the substratum provides strong selection for rapid reproduction on seagrasses. Not only is the substratum short-lived relative to rocks, but there is considerable variation in life-expectancy among seagrass tips, depending on herbivory, leaf age, and storms. The short planktonic period of larvae allows population differentiation over relatively small scales, since most rocky reefs in the northern Gulf of Mexico are in water deep enough for seagrasses to be rare. Thus, larvae are only likely to encounter one kind of substratum, and there should be little genetic exchange between seagrass and rocky reef populations. McKillup and Butler (1979) suggested that species with long planktonic larval periods might have flexible reproductive patterns. Very restricted dispersal is widespread among subtidal sessile animals and some plants (Thorson, 1950, for review), and population differentiation of reproductive patterns, rather than flexibility, may be more common in these organisms.

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